

# Potential migratory routes of *Urania boisduvalii* (Lepidoptera: Uraniidae) among host plant populations

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## Abstract

**Aim:** Migratory species depend on various habitats and resources along their migration routes. Characteristics such as dependence on distinct habitats and the presence of multiple threats along their migratory routes make these species vulnerable, and gaps in knowledge about their ecology and migration processes make them difficult to conserve. *Urania boisduvalii* is a diurnal moth endemic to Cuba that feeds on plants of *Omphalea* spp. during its larval phases. These plants produce secondary metabolites as a defence against the moth's larvae, which then are forced to migrate. Although some ecological aspects of *Urania boisduvalii* are known, its migration routes remain largely unknown. This research proposes potential migratory routes of *Urania boisduvalii* among populations of its host plant.

**Location:** Cuba.

**Methods:** We developed ecological niche models of the moth and its hosts based on environmental, anthropic, biotic and biogeographic factors to obtain potential distributional areas that include zones where positive interactions are found but exclude those where negative factors are present. These areas were overlapped to hypothesize potential breeding areas for the moths. Potential migratory corridors were proposed based on environmental connectivity.

**Results:** The moth and its hosts have broad potential distributions; however, limiting factors have substantially reduced these areas, especially for plants. The potential migratory routes of *Urania boisduvalii* are complex and mostly involve the western and eastern regions of Cuba. Most records outside potential breeding areas were close to these migratory corridors.

**Main conclusions:** We offer initial hypotheses of the migratory routes of *U. boisduvalii*, which may be useful to guiding monitoring projects that can provide more definitive views of the seasonal distribution of this species across the Cuban archipelago.

## KEYWORDS

distributions models, diurnal moth, ecological niche, migratory insects, *Omphalea*, Uraniinae

## 1 | INTRODUCTION

The genus *Urania* Fabricius is unique to the Neotropics (Smith, 1991), currently comprising three species of migratory moths, with a fourth already extinct (Lees & Smith, 1991; Meerman & Boomsma, 1997; Nazari, Schmidt, Prosser, & Hebert, 2016; Smith, 1983; Williams, 1937, 1958; Young, 1970). This genus feeds exclusively on plants of the genus *Omphalea* (Euphorbiaceae) (Lees & Smith, 1991). Host plants that have been predated upon by various generations of *Urania*'s caterpillars may increase their concentration of secondary defensive chemical compounds, forcing these moths to seek new sources of food (Kite, Scofield, Lees, Hughes, & Smith, 1996; Lees & Smith, 1991; Smith, 1991). Therefore, the migration of these moths has been attributed to the periodic search for food for their larval stages (Smith, 1983). Previous research aiming to understand and describe the migratory routes for these moths indicated that they need several alternating host populations for survival (Lees & Smith, 1991; Meerman & Boomsma, 1997; Smith, 1991; Williams, 1937; Young, 1970).

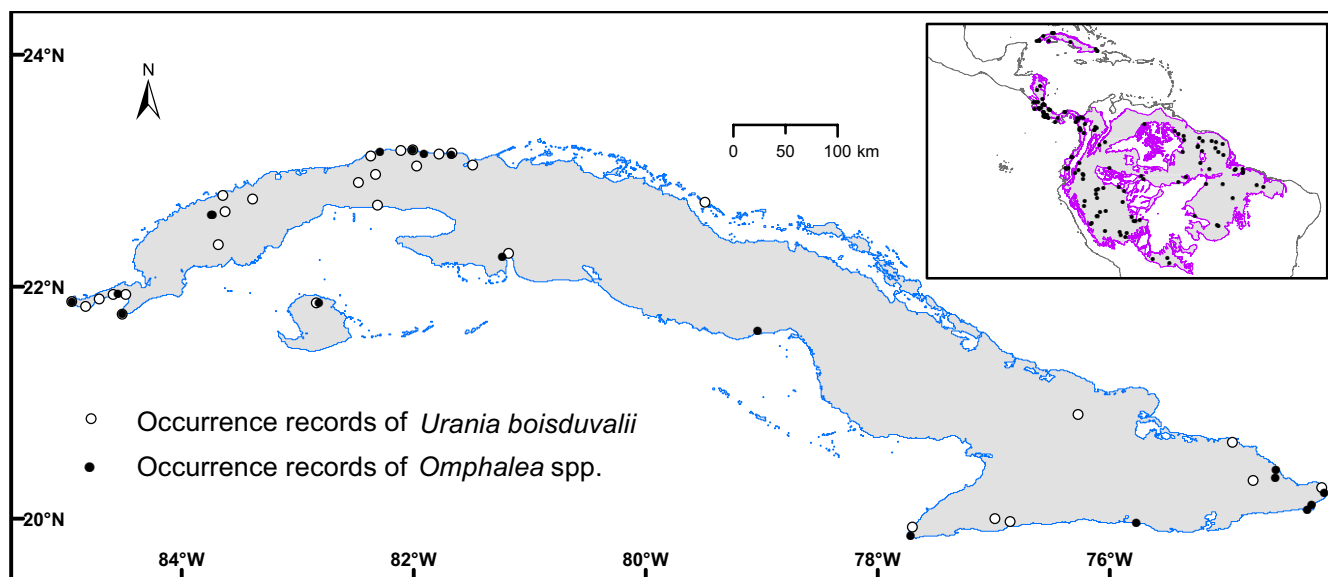
The genus *Urania* is represented in Cuba by two endemic taxa, *U. fulgens poeyi* (Herrich-Schäffer), with a distribution restricted to only two localities in eastern Cuba (Lees & Smith, 1991), and *U. boisduvalii* (Guérin), with a pan-Cuban distribution (Barro & Rodríguez, 2005). The first study related to *U. boisduvalii* dates back to the beginning of the 19th century (MacLeay, 1834). MacLeay described the morphology of different phases of the life cycle of this moth and some elements of its behaviour. Other authors developed studies on more details of their life cycle and behaviour, host plants, tympanic organs and phylogenetic relatedness (Barro, 2006; Barro & Rodríguez, 2005; Barro, Vater, Pérez, & Coro, 2009; Lees & Smith, 1991; Nazari et al., 2016; Smith, 1991). Most adult *U. boisduvalii* have been observed near the coasts,

as well as in karstic areas, in association with their host plants. *Omphalea* is represented in Cuba by three species (Greuter & Rankin, 2016), two endemic to the country (*O. hypoleuca* Griseb. and *O. trichotoma* Muell. Arg.), as well as one, *O. diandra* L., with a broad distribution in the Neotropical region (Lees & Smith, 1991). These plants are largely confined to karstic and coastal areas in Cuba (Alain, 1953).

Many coastal karstic zones in Cuba are under pressure from oil extraction activities and tourism infrastructure development (Camacho, Baena, & Leyva, 2010). The degradation of these habitats is affecting populations of *Omphalea* and thus potentially threatening populations of *Urania* (Meerman & Boomsma, 1997; Williams, 1937). Different larval stages of *U. boisduvalii* use plants of different maturity levels (Barro, 2006); hence, *Omphalea* populations must also have good structural complexity. Lees and Smith (1991) reported that populations of *U. boisduvalii* are decreasing, perhaps due to host population declines (Nadkarni & Wheelwright, 2000).

The migration of *Urania boisduvalii* has been minimally documented; Smith (1991) mentioned north–south movements. However, recent field observations also suggested that *U. boisduvalii* migrates in west–east directions. Although the direction of migration detected in recent observations coincides with the shape of the archipelago and with the direction of wind currents, information about this phenomenon remains incomplete. However, one might hypothesize that migratory routes between populations of host plants take place through favourable climate regions (Drake & Farrow, 1988; Sparks, Roy, & Dennis, 2005).

The aim of this work was to propose potential migratory routes of *Urania boisduvalii* among populations of its host plants across the Cuban archipelago. Ecological niche modelling and GIS analyses were used to generate potential migration corridors based on environmental connectivity across the country.



**FIGURE 1** Study area. Inset, location of the Cuban archipelago in the Neotropics. *Omphalea* spp. records represent the three species in Cuba: *O. hypoleuca*, *O. trichotoma* and *O. diandra*. Blue outlines surround hypothesized accessible areas (calibration areas) for *U. boisduvalii*, and purple outlines surround hypothesized accessible areas for *Omphalea* spp

## 2 | METHODS

### 2.1 | Study area

The study area was the Cuban archipelago (Figure 1), which has an area of ~110,922 km<sup>2</sup> and a very complex geological history (Formel, 1989). Most of Cuba has a flat topography, with higher elevations restricted to four mountain systems (Díaz, 1989). The proximity of the archipelago to the mainland as well as its topography dictates its moderate tropical climate (Díaz, 1989).

### 2.2 | Occurrence and environmental data

Occurrence records for *U. boisduvalii* (49), *O. hypoleuca* (1), *O. trichotoma* (16) and *O. diandra* (256) were obtained from the scientific literature (Aborrezco, 1995; Barro, 2006; Barro & Rodríguez, 2005, 2006; Capote, García, Urbino, & Senli, 1988; Claro & Rodríguez, 1989; González-Torres et al., 2016; Lees & Smith, 1991; Rosete, Herrera, & Ricardo, 2004; Vilamajó & Martínez, 2005; Vilamajó, Ricardo, Capote, González, & Cabrera, 2010), the collection and the herbarium of the Institute of Ecology and Systematics (IES-HAC, Cuba), the National Botanic Garden of Cuba (HAJB), the Global Biodiversity Information Facility database (GBIF; [www.gbif.org](http://www.gbif.org)), the Catalog of Vascular Plants of the Botanical Garden of New York, field notes from one author of this paper (AB) and recent field sampling by HAJB. Only occurrences reported after 1950 and with no inconsistencies were kept. Records of the three plant species in Cuba were pooled to create niche models for the three species together. This pooling was based on the existence of niche overlap among Cuban species of *Omphalea* and *O. diandra*, which was evaluated using the similarity test of Broennimann et al. (2012). We used the occurrence records of the three plant species along the two first principal components of a PCA calibrated with bioclimatic variables (see variable selection in model calibration and evaluation below) in the "ENMTools" package (Warren, Dinnage, & Matzke, 2017) from R 3.4.1 (R Core Team, 2017).

To avoid autocorrelation, a spatial thinning of occurrences was performed, leaving gaps of ≥5 km between records. This distance was chosen based on the spatial resolution of the environmental variables (~1 km), as well as the species ecology and the environmental heterogeneity across Cuba (Radosavljevic & Anderson, 2014). This procedure resulted in 30 occurrences for *U. boisduvalii*, 1 for *O. hypoleuca*, 14 for *O. trichotoma* and 133 for *O. diandra*, and was performed in the "spThin" R package (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015).

As environmental predictors, bioclimatic variables were used from the WorldClim database at a spatial resolution of 30" (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Variables combining temperature and precipitation were excluded because they have spatial artefacts between adjacent grid cells (Escobar, Lira-Noriega, Medina-Vogel, & Peterson, 2014). The suitability layer for *Omphalea* plants was used as a predictor in the model for *U. boisduvalii* distribution considering the known interaction between these species

(Araújo, Marcondes-Machado, & Costa, 2014; Giannini, Chapman, Saraiva, Alves-dos-Santos, & Biesmeijer, 2013). Aridity was also considered an environmental predictor for *Omphalea* spp. and was obtained from the CGIAR-CSI Global-Aridity and Global-PET database at the same resolution (available at <https://cgiarcsi.community/data/global-aridity-and-pet-database/>).

### 2.3 | Model calibration and evaluation

The calibration area for the *U. boisduvalii* model was the entire Cuban archipelago. For the plants, this included all ecoregions known to be occupied by the three species (Figure 1). Ecoregions were identified using the world map of terrestrial ecoregions (Olson & Dinerstein, 2002). For all model development, 10,000 random points were used as background data to create niche models.

To select the best set of predictors for characterizing the species' niche, an exploration of the performance of multiple models was created with different parameter settings using the "MaxentVariableSelection" R package (Jueterbock, Smolina, Coyer, & Hoarau, 2016) for a total of 46 models for the moth and 85 for the plants. Models were created with 12 regularization multiplier values (0.5 to 6, at intervals of 0.5), one setting of feature classes (linear, quadratic and product; LQP) and different sets of environmental variables. The best sets of variables were chosen by determining the model with the best performances and selecting predictors with contributions ≥1% and correlations below 0.8 (see Supporting Information Appendix S1).

To define an adequate level of complexity, different configurations of Maxent were evaluated by comparing the performances of 48 test models. These models were created using the checkerboard method for partitioning training and test data, eight regularization multiplier values (0.5–4, with intervals of 0.5) and six settings of feature classes: L, LQ, H, LQH, LQHP and LQHPT (where L = linear, Q = quadratic, H = hinge, P = product and T = threshold). These analyses were performed using the "ENMeval" R package (Muscarella et al., 2014). Best configurations were selected based on significance ( $p \leq 0.05$ ), adequate correspondence between expected and resulting omission rates, and low values of the corrected Akaike Information Criterion (AICc).

Final models were calibrated with the full set of thinned records (30 for *U. boisduvalii* and 147 for *Omphalea* plants; see Supporting Information Appendix S2) and the selected sets of variables (4 for the moth and 10 for the host plants; Supporting Information Appendix S1 provides details). Modelling was performed in Maxent 3.4.1 with 50 bootstrap replicates, and the best configurations obtained during the evaluation process (see Section 3). Final models for both species were projected only to the Cuban Archipelago, and clamping and extrapolation were not allowed.

### 2.4 | Refining models

We used the average of the suitability values corresponding to 5% of the occurrence data with the lowest suitability levels to convert

continuous models to binary ones. The presence of negative environmental characteristics, local environmental changes produced by human activities, possible geographic barriers and negative biotic interactions were considered to obtain approximations to the actual areas of distribution of these species (Anderson, 2015).

All soil types in which the three *Omphalea* species have been reported (suitable soils) and that are present in Cuba (as in Nuñez-Penicher, Cobos, Amaro, & Barro, 2016) were identified using the SoilGrids Soil Map of the World (spatial resolution 250 m; available at [https://soilgrids.org/#/?layer=TAXNWRB\\_250m&vector=1](https://soilgrids.org/#/?layer=TAXNWRB_250m&vector=1); Hengl et al., 2017, 2014). Soil types other than suitable soils were defined as negative environmental characteristics for the plants. For both the plants and the moth, areas without vegetation cover, identified using information from the Global Forest Change database (Hansen et al., 2013); areas covered by water bodies; and urbanized areas were also removed (Cuban land use map, Hernández, Pérez, Bosch, & Rivero, 1999). Productive areas were only included as restrictors for the plants (Hernández et al., 1999). As a biogeographic barrier, an elevational limit of 1,000 m was used for both *U. boisduvalii* and *Omphalea* spp. considering the maximum elevation at which this moth has been recorded. This restriction was imposed via a Digital Elevation Model (DEM; resolution 30 m) derived from the Shuttle Radar Topography Mission (<https://doi.org/10.5066/F71835S6>). As biotic negative interactions for both the moth and the plants, mangrove, swamp, uncovered and semi-uncovered areas were considered. Pine forests and savannas were added as negative interactions only for the plants. These cover types were selected using the vegetation cover map of Estrada et al. (2011). The complete model restriction process was performed using ArcGIS 10.5.1.

## 2.5 | Potential migration routes of *Urania boisduvalii*

Considering that breeding areas are zones where eggs hatch, larvae develop and adults emerge (Johnson, 1969), to estimate these areas for *U. boisduvalii*, its restricted potential distributional areas and those of *Omphalea* plants were overlapped. Potential migratory routes of *U. boisduvalii* among its breeding areas were identified by calculating least-cost corridors based on environmental connectivity. To do so, the moth's suitability layer was transformed into a friction layer (resistance to displacement; 0–1 and 10 values) by inverting the values of suitability. Therefore, sites with greater suitability presented low resistance and vice versa; ocean was characterized as maximum resistance (values of 10). Using this layer and moth occurrences inside and  $\leq 1$  km from potential breeding areas, likely corridors for *U. boisduvalii* migration were generated. Other potential corridors were generated using the friction layer and 10 distinct sets of random points (26 points each) to extrapolate potential migration routes based more in the ecological niche model than in the actual records. These points were randomly generated within potential breeding areas. The corridors generated by the ten sets of random points were summed. The corridors with the highest values of connectivity in the result of the sum and the results generated with actual occurrences were

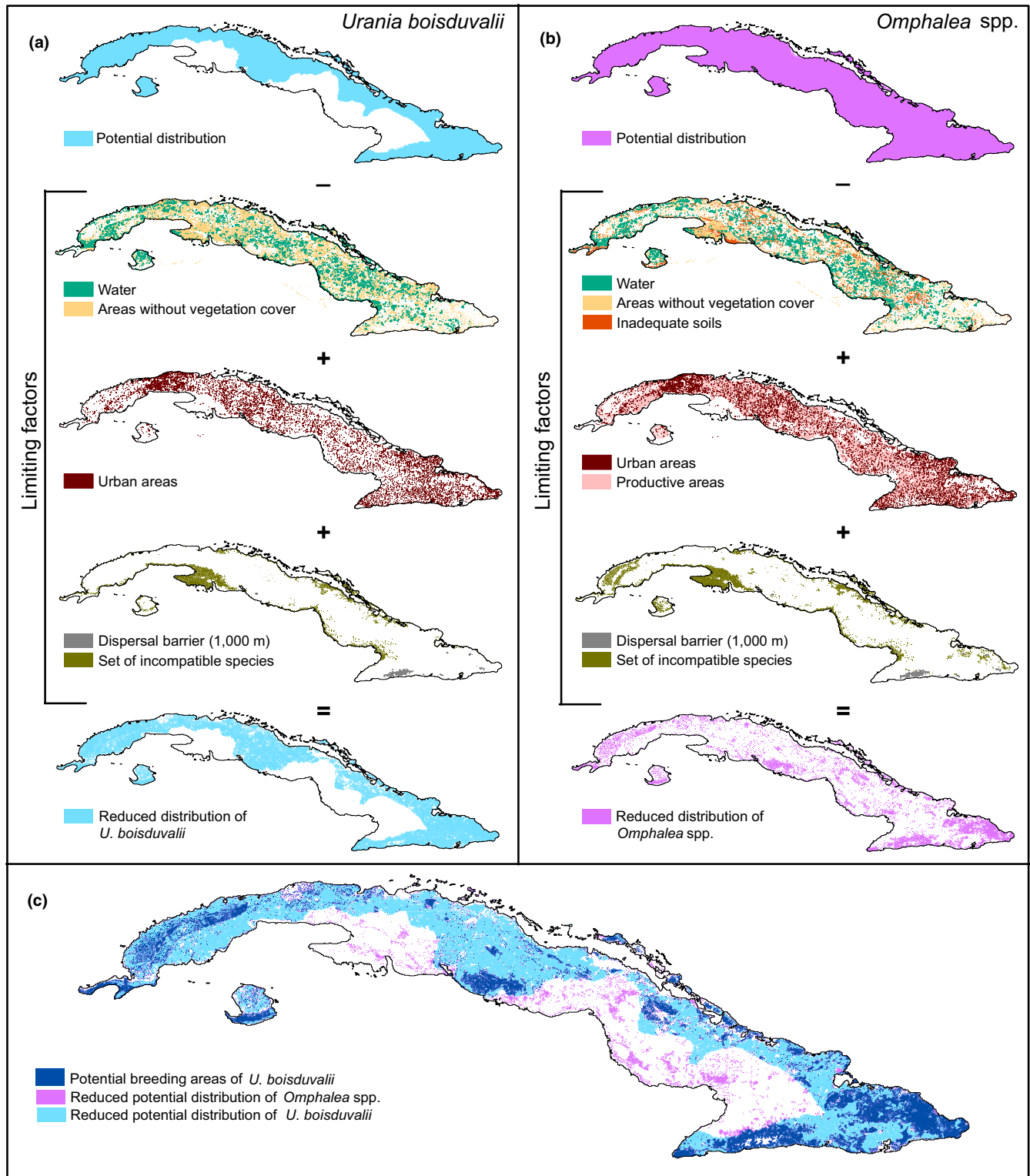
considered the most probable migration routes. These processes were performed using ArcGIS with the "SDMtoolbox" extension (Brown, 2014).

## 3 | RESULTS

The background similarity test among the plants was not able to reject the hypothesis of niche similarity (Schoener's  $D = 4.98 \times 10^{-3}$ ,  $p = 0.29$ ); thus, niches of *O. diandra* and the Cuban endemic *Omphalea* species overlap in environmental space (Appendix 3). All of the models for *U. boisduvalii* and *Omphalea* spp. predicted independent data significantly better than random expectations, but they differed in AICc values and omission rates (Supporting Information Appendix S4). The best values of AICc resulted from regularization multipliers of 2 and 3.5, as well as H, LQHP and LQH feature classes for the moth. Best values for the plants were found with regularization multipliers of 2.5 and 2, as well as LQHPT and LQH feature classes. Best correspondence between the expected and resulting omission rates was obtained with regularization multipliers of 1.5, 2.5 and 3.5, as well as LQH feature classes for the moth. For the plants, the regularization multipliers were 3.5 and 4, as well as H features only. The selected parameters for *U. boisduvalii* were a regularization multiplier of 3.5 and LQH feature classes, whereas for *Omphalea*, a regularization multiplier of 2.5 and LQHPT feature classes were chosen.

Final models for both species were significantly better than random expectations, with omission rates of  $\sim 0.03$  for both *U. boisduvalii* and *Omphalea* spp. Variables with the highest contributions to the moth and plant models were BIO17 (Precipitation of Driest Quarter) and BIO13 (Precipitation of Wettest Month), respectively (other variable contributions are listed in Supporting Information Appendix S1). The suitability layer for *Omphalea* spp. contributed 11.4% to the moth model. The AICc value of the moth model that included the plant's suitability layer was more than 40 units lower. The moth's potential distributional area (71,590 km<sup>2</sup>,  $\sim 66\%$  of the archipelago) has an irregular shape and is without fragmentation in the northern part of the entire main island. This area occupies almost all of nearby Isla de la Juventud. The potential distribution range of the three species corresponded to 100% of the archipelago (110,922 km<sup>2</sup>).

Environmental and anthropogenic factors likely limiting the species' potential distributions were widespread through the archipelago, whereas biotic factors were concentrated in wetlands and mountain ranges (Figure 2a,b). Moth and plant potential distributions were reduced by 23% and 84%, respectively (Table 1, Figure 2). The factors that most restricted the potential distributions of *U. boisduvalii* and *Omphalea* spp. were areas without vegetation cover (17%) and productive areas (48%), respectively. After restriction, potential distributional areas for the moth and plants decreased to 54,855 and 20,534 km<sup>2</sup>, respectively. Potential breeding areas (i.e., the area of overlap between the two restricted potential distributions) had a fragmented pattern across the archipelago, with an area of 15,797 km<sup>2</sup> ( $\sim 15\%$  of Cuba). Higher values of environmental



**FIGURE 2** Potential distribution and model refining process for *Urania boisduvalii* (a) and *Omphalea* spp. (b). Potential breeding areas of *U. boisduvalii* (c) obtained from overlapping the species' restricted models

resistance for the moth on the main island of the archipelago were associated with lowlands (Figure 3). Environmental connectivity was higher in the central and western regions of the archipelago, and principally in the northern portion of the main island. Potential migration routes for the moth were denser in the western and eastern

regions than in the central region (Figure 4). Routes simulated with actual occurrences had the lowest costs in the western region of the archipelago and a single corridor extending across most of the central region, connecting western with eastern populations of *U. boisduvalii* (Figure 4a). Summed potential migration routes presented a



larger number of routes, especially in the central and eastern region; however, the southern part of the central region remained weakly connected (Figure 4b).

**TABLE 1** Potential distributional areas of *Urania boisduvalii* and *Omphalea* spp. restricted by the limiting factors in the Cuban archipelago. The percent values are in function of the species potential area

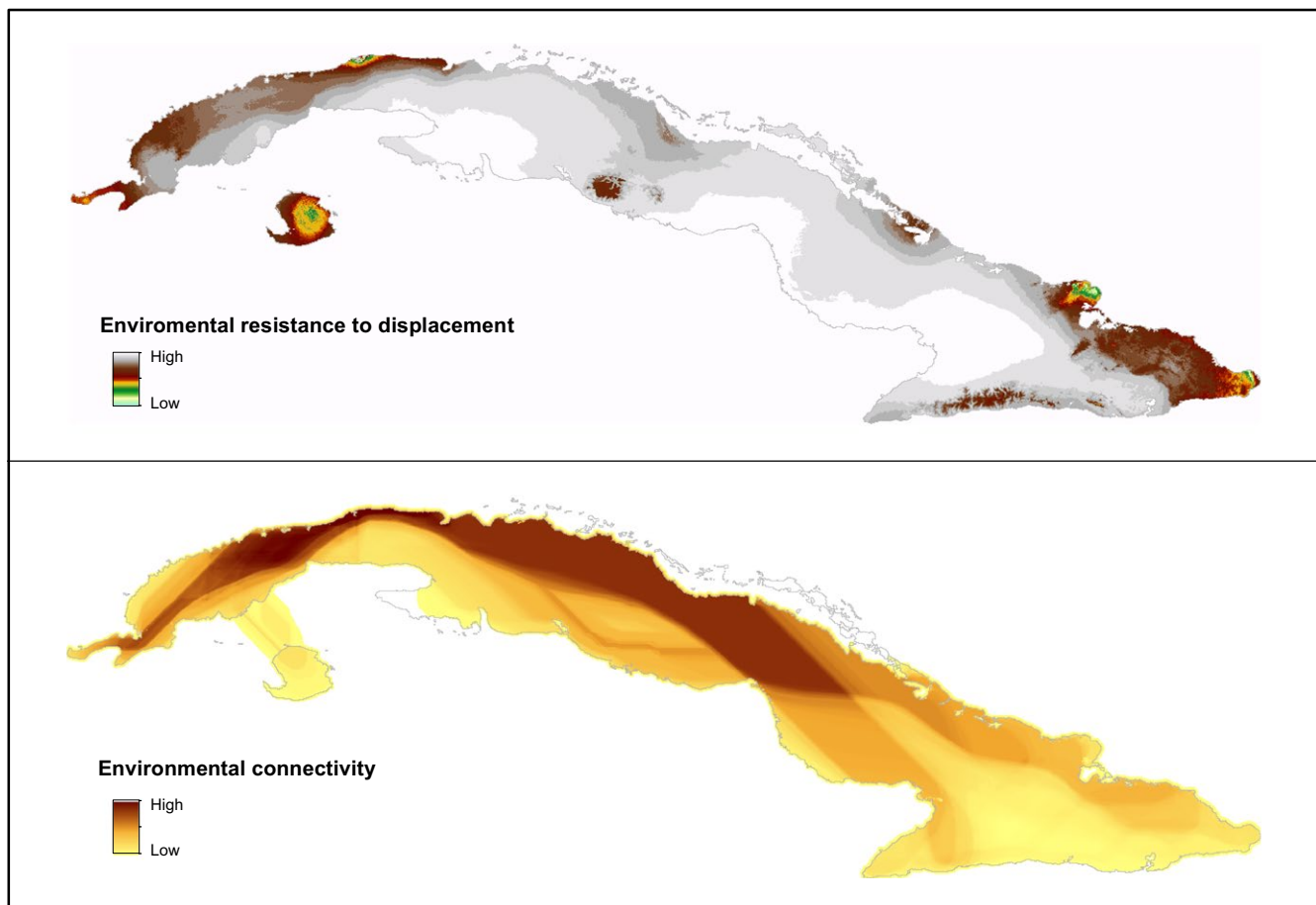
Limiting factors	<i>Urania boisduvalii</i>		<i>Omphalea</i> spp.	
	km <sup>2</sup>	%	km <sup>2</sup>	%
Water	1,184	1.65	1,825	1.68
Areas without vegetation cover	12,340	17.24	20,155	18.51
Inadequate soils	–	–	6,011	5.52
Urban areas	569	0.80	772	0.71
Productive areas	–	–	52,177	47.9
Dispersal barrier (1,000 m)	307	0.43	307	0.28
Set of incompatible species	2,334	3.26	7,119	6.54

## 4 | DISCUSSION

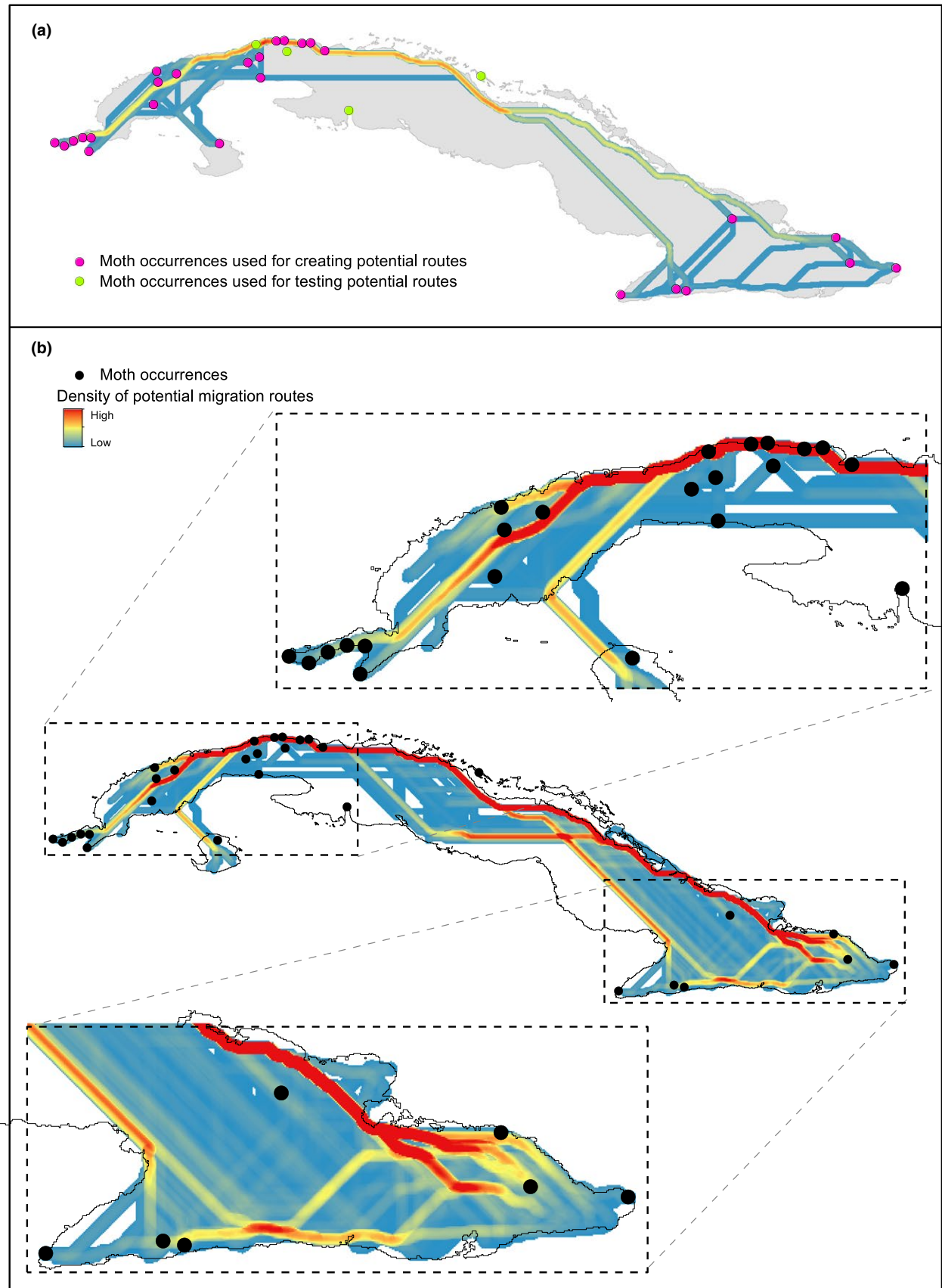
### 4.1 | Potential distribution models

The limited number of records for the *Omphalea* species endemic to Cuba did not allow modelling their individual niches. However, because niches of *O. diandra* and the Cuban endemic species were similar, grouping occurrences of the three allowed better characterization of their potential distribution across the archipelago. A similar approach has been recently suggested by Qiao, Peterson, Ji, and Hu (2017) in which the authors proposed that models for species with restricted distributions can be improved using occurrences of related species if their niches overlap (e.g., Cobos & Alonso Bosh, 2018).

Model evaluation and selection results indicated that best correspondence between expected and resulting omission rates was not found in models with the lowest AICc values. Similar findings have been previously reported (Atauchi, Peterson, & Flanagan, 2018; Nuñez-Penichet et al., 2016); these findings signal potential problems in selecting models based only on minimum complexity. In this case, the model with the best omission rates correspondence was selected for *U. boisduvalii*, as we had high confidence in the accuracy of occurrences. For *Omphalea*, the model with the lowest complexity was chosen due to a lack of complete certainty in the occurrences.



**FIGURE 3** Friction layer (environmental resistance to displacement) and environmental connectivity across the Cuban archipelago. Friction values range from 0 to 10 (0–1 in land and 10 in ocean)



**FIGURE 4** Proposed potential migratory routes for *Urania boisduvalii* across the Cuban archipelago based on the species ecological niche models. Routes simulated with the actual occurrences of the moth (a) and routes simulated with the 10 sets of 26 random points each generated inside the potential breeding areas of the moth (b)

The two sets of final models resulted in similar omission rates despite the fact that their configurations were chosen based on distinct model performance indicators. Models for the moth improved in AICc after adding the suitability layer for the plants despite greater complexity, which supports the notion that this layer is an indicator of a positive biotic interaction.

The potential distribution of *U. boisduvalii* is widespread through the archipelago and includes most of the highland areas (Figure 2a). This range excludes most of the southern portion of the main island, indicating that those areas are not suitable for the species. However, one record in the west-central part of the main island was omitted by this model (Figure 1), likely related to the selected threshold, which aimed to exclude outliers. Although the omitted record may be considered as an outlier or a vagrant record, the presence of the host plant in the vicinity suggests that this record may be correct.

The potential distributional area of the *Omphalea* species obtained in this research is broader than that presented by Nuñez-Penicher et al. (2016) (Figure 2b). The difference derives from the use of software and protocols capable of identifying the best combinations of variables and parameters in the current study, which yields a different variable set, regularization multipliers (higher complexity in the current research) and presence thresholds (lower presence threshold in this case). Further, in this study, more occurrence records of *O. trichotoma* and *O. diandra* from Cuba were included. That the potential distribution of this species covers the entire archipelago is not surprising considering that the niche breadth of the Neotropical species of this genus is likely wider than the niche of the Cuban species. Because Cuba is a tropical archipelago and its climate is mostly stable (Díaz, 1989), climates sampled by *O. diandra* in other parts of the Neotropics may include all of the Cuban climatic variation.

## 4.2 | Restriction of species' potential distributions

Estimating distributional areas may require the use of more than just climatic variables (Austin & Van Niel, 2010), demanding a step of excluding areas known to be impossible for the species to colonize (Anderson, 2015). In this study, only climatic variables were considered in developing models due to coarse spatial resolution of the occurrence data, as well as to their temporal heterogeneity. Therefore, our restriction processes allowed better approximations to the species distributions. All of the limiting factors used to restrict the potential distributional areas were categorical in nature, which can considerably complicate the modelling process (Ortega-Huerta & Peterson, 2008).

Overall, the potential distribution of host plants was affected more drastically by limiting factors compared with those that affected the moth's. Plants are affected highly by land use change (e.g., forest converted to agricultural areas or pasturelands), whereas a moth may have more flexibility at least during its adult stage, using various habitats, including anthropogenic ones (Barro, 2006; Lees & Smith, 1991; Macleay, 1834; Smith, 1991). However, although

adult *Urania* can feed on the nectar of plants other than *Omphalea* (e.g., species of the families Lauraceae, Mimosaceae, Combretaceae, Solanaceae, Ehretiaceae and Verbenaceae; MacLeay, 1834; Lees & Smith, 1991; Barro & Rodríguez, 2005), the strict dependence of their larvae on *Omphalea* plants makes the moth face similar risks than its host. The strong effects shown by land use changes affecting host plant distribution can provide information on the importance of protecting areas with natural land cover, not only for these plant species but also for the conservation of the moth. Notably, habitat degradation was the main factor that led to the extinction of its sister species *U. sloanus* in Jamaica (Lees & Smith, 1991).

Potential distributional areas for the moth and its hosts were predicted for the central parts of the archipelago. Sampling is needed to assess the presence of these species in the region: if new occurrences are found, they may help complete the representation of the species' distribution in Cuba.

## 4.3 | Potential breeding areas and migratory routes of *Urania boisduvalii*

The obtained breeding areas for *U. boisduvalii* estimated in this study were substantially smaller and more fragmented compared with its reduced potential distribution (Figure 2c) due to our step of overlapping with the estimated distribution of *Omphalea* spp. (~19% of the Cuban archipelago, and highly fragmented). These breeding areas, as with the reduced potential distribution of the moth and the plants, include areas in central Cuba, underscoring the need for more sampling in that region.

If the degree of suitability in environmental conditions is considered, potential migratory routes have different orientations: not only north-south or west-east as previously suggested (Figure 4). Only monitoring can confirm which routes and at what times these routes are used or whether *U. boisduvalii* changes its migration direction depending on the season. Something similar has been observed by Williams (1937, 1958), who documented that the migration of *U. fulgens fulgens* was north to south in March and April and west to east in June to September.

Occurrences of the moth that did not coincide with potential breeding areas and the reduced potential distribution of *Omphalea* spp. were likely due to the detection of individuals during migration. Most of those records were <20 km away from the migration routes estimated with actual occurrences, except for one from the southern coast in the central-western region (Figure 4a). This proximity to the predicted corridors and potential routes generated based on the potential breeding areas of the moth (i.e., the sum of routes modelled with the actual records and with the random points inside breeding areas; Figure 4b) support the notion that this species migrates according to climatic suitability in the archipelago. Indeed, temperature has been recognized as an important factor for insect flight (Johnson, 1969). Drake and Reynolds (2012) also found that temperature determines if flight can be maintained and that it limits the range of heights over which sustained flight is possible.



Some of the potential migratory routes cross areas above 1,000 m, elevations at which no individuals of this species have been recorded (Aborrezco, 1995; Barro, 2006; Barro & Rodríguez, 2005; Lees & Smith, 1991). However, *U. f. fulgens* has been reported at elevations ranging from 3 to 1,000 m (Williams, 1937) and even up to 2,000 m of altitude (Murillo-Hiller, 2008). Another migratory Lepidoptera, *Danaus plexippus*, can also fly at higher elevations than normal during migration when the wind direction is favourable (Gibo, 1981). Perhaps *U. boisduvalii* uses the highest mountains of Eastern Cuba as a migratory route when favourable wind conditions are present.

## 5 | CONCLUSION

Most of Cuba was found to be suitable climatically for the species studied. However, other limiting factors—including anthropogenic ones—considerably reduced potential distributions, especially the distributions of the plants. The modelled distributions of the species in Central Cuba had high uncertainty, making further sampling in this zone a priority to corroborate and improve the models. These efforts can focus on the restricted potential distributional areas obtained in this research, although localities omitted by the potential moth distribution model should not be discarded.

The potential migratory routes proposed in this contribution suggest that the direction of this process may be more complex than previously thought. Although the potential migratory routes generated in this study are only hypotheses for this moth's movements, they are a good starting point to begin monitoring the migration of this species. Data documenting this species' movements are crucial for testing and improving models, as well as for laying a foundation for future studies of this moth's migration. Next steps aiming to explain this species' migration may also find these results useful in identifying initial targets for monitoring.

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## DATA ACCESSIBILITY

The data are provided in the Supporting Information.

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#### BIOSKETCH

The authors' research interests include the ecology and evolution of biotic interactions, avian and plant ecology, global change biology, biogeography and biodiversity conservation. Research interests of this group include ecology, biogeography, modelling of distributions, conservation, and diversity of Lepidoptera, their interactions with host plants, as well as potential threats from global change on this and other systems.

Author contributions: CNP, MEC and AB designed the study; CNP and AB collected the data; CNP, MEC and JS performed the analyses and wrote the manuscript. All the authors revised and edited the last version of the manuscript.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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